BREAKDOWN OF KAMAHI LEAVES IN FOUR SOUTH WESTLAND STREAMS

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ABSTRACT

Breakdown of kamahi (*Weinmannia racemosa*) leaves enclosed in 1 mm mesh bags was investigated in two acid, brown-water and two circumneutral, clear-water streams in South Westland, New Zealand. Decay coefficients (-k) calculated from data including day 0 showed that leaves broke down faster in clear-water (-k = 0.0039 and 0.0034) than in brown-water streams (-k = 0.0026 and 0.0022). Scanning electron microscope examination of leaf surfaces after 148 days incubation revealed that fungi were common on leaves from the brown-water sites, but that hyphae often were associated with amorphous material which accumulated on leaf surfaces. Bacteria appeared to be more common on leaves from the clear-water streams. Microbial respiration rates on leaves measured on two dates ranged from 24.8 to 73.4 $\mu gO_2.g^{-1}dw.h^{-1}$ but no clear pattern between sites was evident. Invertebrate faunas colonising leaf bags were dominated by chironomids at the brown-water sites (≈ 90% of the total fauna) and very few large particle detritivores were present. In contrast, obligate (*Triplectides* sp.) and facultative (*Austroperla cyrene*, *Oeconesus* sp. and *Olinga feredayi*) shredders made up 8-38% of invertebrate colonists at the clear-water sites, and appeared to be largely responsible for the faster breakdown rates recorded there.

KEYWORDS: kamahi, *Weinmannia racemosa*, Cunoniaceae, acid streams, brown-water streams, South Westland, leaf breakdown, microbial respiration rates, invertebrate feeding

INTRODUCTION

Allochthonous leaf litter represents a substantial proportion (as much as 90%) of the energy input to many forested headwater streams (Fisher & Likens, 1973; Cummins, 1974). After initial leaching of soluble compounds, leaf breakdown is affected by abiotic fragmentation, microbial decomposition and invertebrate feeding (Kaushik & Hynes, 1971; Petersen & Cummins, 1974). Factors which affect the rates at which leaves breakdown in streams include water temperature, leaf "toughness" and aspects of stream water chemistry including pH (Petersen & Cummins, 1974; Burton et al., 1985; Chamier, 1987). The recent acidification of many Northern Hemisphere surface waters by acid rain has focussed attention on the effects of pH on leaf litter breakdown, and several studies have shown that decomposition is slower in acidic conditions (e.g., Hildrew et al., 1984; Allard & Moreau, 1986), partly because of lower microbial activity.

On the west coast of the South Island, many lowland streams are stained brown by organic acids of terrestrial origin which can lower water pH to about 4 (Winterbourn & Collier, 1987). To determine whether "naturally" as opposed to anthropogenically derived acidity affects leaf litter breakdown, we compared weight losses, microbial activity and invertebrate colonisation of kamahi (*Weinmannia racemosa*: Cunoniaceae) leaves in two acid, brown-water streams and in two nearby clear-water streams of circumneutral pH.

STUDY AREA

The study was carried out between March 1985 and January 1986 in two brown-water and two clear-water streams in the Okarito/Franz Josef region of South Westland. A detailed description of the four sites as well as details of their water chemistry, physical characteristics and benthic invertebrate populations are given by Collier & Winterbourn (1987). The two brown-water streams, Steep Creek and Suspect Stream (NZMS1 S71 870896 and 864902, respectively) have a pH of 4.3-5.7 and are stained by high concentrations of dissolved organic carbon (DOC) (6.6-16.3 $g.m^{-3}$). In contrast, Hidden Creek and Toilet Stream (NZMS1 S71 823671 and 821677, respectively) have circumneutral pH (6.6-8.0) and clear waters with low concentrations of DOC (0.3-4.7 $g.m^{-3}$).

Riparian vegetation at the clear-water sites was predominantly wineberry (*Aristotelia serrata*), tutu (*Coriaria arborea*) and pate (*Schefflera digitata*). At Steep Creek, stream-side vegetation was mostly kamahi (*Weinmannia racemosa*), rimu (*Dacrydium cupressinum*) and the ferns *Cyathea smithii* and *Blechnum discolor*, whereas manuka (*Leptospermum scoparium*) was predominant at Suspect Stream. Very little leaf litter was retained for long in Toilet Stream, Steep Creek or Suspect Stream, but in Hidden Creek where flows were comparatively stable, many leaves were trapped by branches and emergent rocks and at times substantial accumulations were found.

Water temperature regimes were similar at Toilet Stream, Steep Creek and Suspect Stream (range 4-17^{o}C), but at Hidden Creek which is spring-fed, the range was only 8 to 12^{o}C (Collier & Winterbourn, 1987).

METHODS

LEAF BAGS:

Kamahi leaves were collected from a single tree near Okarito in January 1985 and returned to the laboratory where 15 g ($\pm$ 0.005 g) of fresh leaf material were placed in each of 53 1 mm mesh bags (15 x 12 cm). All bags were heat-sealed and dried for seven days at 50^{o}C. Dry kamahi leaves are very brittle, and therefore only five of the bags were reweighed to estimate the initial dry weight of leaves ($\bar{x} \pm SE$ = 7.049 $\pm$ 0.091 g). On 25-27 March 1985, 12 bags were placed in each of the four study streams in commercial grade onion sacks which were anchored with heavy rocks and secured by rope to adjacent trees.

Bags were removed from the streams in sets of three on 9 May, 22 August, 27 November 1985 and 28 January 1986 (i.e., after 42, 148, 244 and 306 days incubation, respectively). All bags were frozen within three hours of collection except in August and September when one bag from each set was kept cool in stream water until microbial respiration rates could be measured (starting eight hours later). In the laboratory, frozen leaves were thawed, washed over a net to collect invertebrates, dried and weighed. Invertebrates were identified and counted.

MICROBIAL RESPIRATION:

Leaves used to measure microbial respiration were washed gently to remove debris and invertebrates, and 0.313-0.990 g (final dry weight) of leaf material was placed in glass respirometers (volume 110 ml, n = 5 per site) containing water (9^o) from the same stream in which the leaves had been held. Experimental and blank respirometers containing water only were sealed with rubber bungs ensuring that no air was trapped inside, and incubated in the dark at 9^oC for 9-11 hours. After incubation, oxygen consumption was measured with a YSI Model 54 O_2 meter and adjusted for respirometer volume. Leaves were frozen and later dried and weighed so that oxygen consumed could be expressed per gram of leaf dry weight.

SCANNING ELECTRON MICROSCOPY:

Leaves removed from the four study streams after 148 days were examined by scanning electron microscopy (SEM). This enabled a qualitative assessment of microbial colonisation and leaf surface breakdown to be made. Sections ($\approx$ 1 cm^2) of leaf were excised immediately after removal from bags and placed in 3% gluteraldehyde fixative in phosphate buffer. Later, they were dehydrated in an alcohol series as described by Rounick & Winterbourn (1983a), air dried and mounted on SEM stubs with double-sided cellotape. After coating with 50 nm of carbon/gold palladium, leaf surfaces were viewed with a Cambridge Stereoscan MK II SEM at magnifications up to 5000 X.

RESULTS

LEAF BREAKDOWN:

By the end of the experiment (306 days), leaves from both clear-water streams were fragmented severely and only the skeletal framework of many remained. Evidence of invertebrate feeding on leaf margins was seen after 148 days (August) at Hidden Creek and, to a lesser degree, at Toilet Stream. In contrast, very little evidence of feeding or skeletonisation was apparent on leaves removed from the brown-water streams and only slight fragmentation had occurred after 306 days.

Losses of initial leaf dry weight were similar at all sites on day 42 (24.6-31.7%), but subsequently leaf breakdown followed the sequence Hidden Creek > Toilet Stream > Steep Creek > Suspect Stream (Fig. 1). By the end of the experiment, only 25% of initial leaf biomass remained in bags from Hidden Creek compared with 60% in bags from Suspect Stream. Statistically significant differences (ANOVA, $P < 0.05$; log transformed data) in dry weights of leaf material remaining were found between Hidden Creek and all other sites on day 148 and day 244, and between pairs of clear-water and brown-water sites on day 306 (Duncan's New Multiple Range test, $P < 0.05$).

Decay coefficients (-k) for leaves were calculated using the exponential decay model of Petersen & Cummins (1974). They calculated -k using a least squares fit of data assuming an asymptote of zero, but this may be inappropriate if rapid initial weight loss is followed by a slow decline in leaf biomass, as at Steep Creek and Suspect Stream. Therefore, we calculated -k values and half lives of leaves with

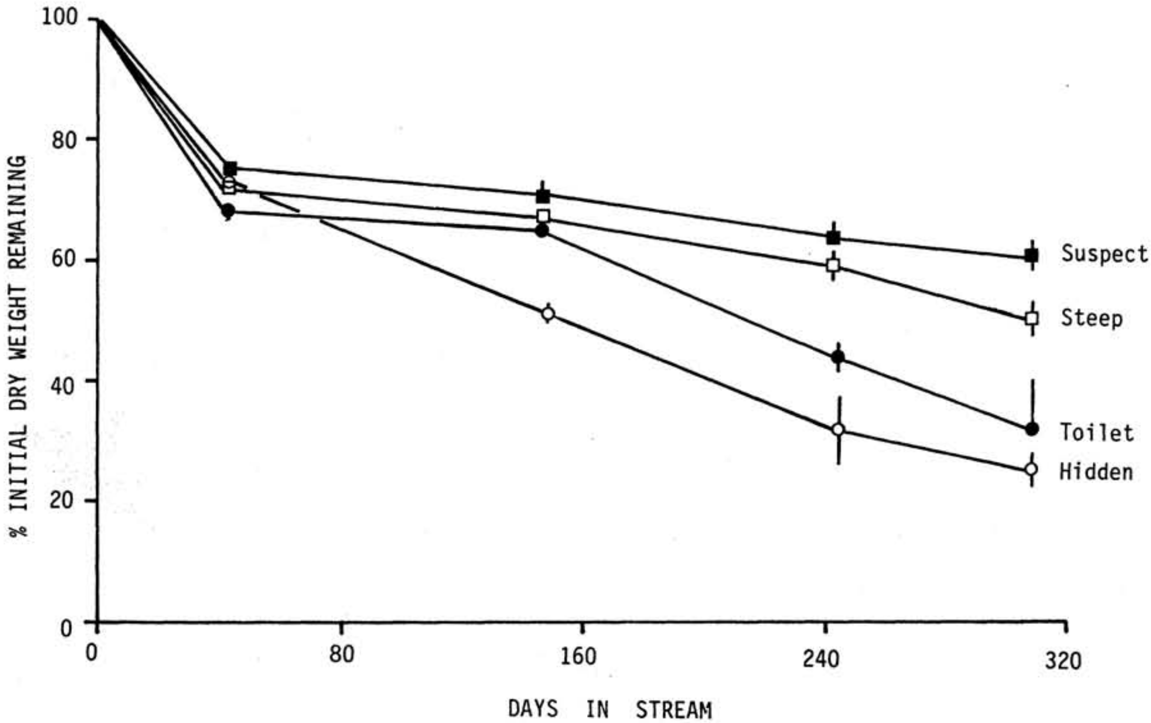


Fig. 1 Percent initial dry weight remaining ($\bar{x} \pm 1$ SE, n = 3) of leaves in 1 mm mesh bags in Hidden Creek (○), Toilet Stream (●), Steep Creek (□) and Suspect Stream (■). Error bars are not shown if included in the symbol.

and without day 0 included in the data set (Table 1). Leaves from the clear-water streams broke down much faster than leaves from the brown-water streams and the differences were even greater when day 0 was excluded from the calculations. Thus, the calculated half-life of leaves from Suspect Stream was 159 days longer when day 0 was excluded.

MICROBIAL RESPIRATION AND ELECTRON MICROSCOPY:

Oxygen uptake rates of microbial communities on leaves removed from the streams in August and November ranged from 24.8 to 73.4 $\mu g.g^{-1}.h^{-1}$ and were higher at all sites in November (Fig. 2). No significant differences (ANOVA, $P > 0.05$, log transformed data) in respiration rates were detected between sites at this time, but in August rates were significantly higher for Hidden Creek and lower for Steep Creek than for any other site (Duncan's New Multiple Range test, $P < 0.05$).

SEM examination of leaf surfaces after 148 days incubation (August) showed that fungi were the main microbial colonisers of leaves at the brown-water sites whereas bacteria tended to be more common at the clear-water sites (Fig. 3). However, fungi were not always associated with leaf surfaces and often were interwoven with amorphous material which tended to accumulate on leaves at the brown-water sites (Fig. 3C). Surfaces of leaves from the clear-water streams were comparatively free of amorphous material, and upper tissue layers had been removed in places (Fig. 3A), perhaps as a result of invertebrates rasping leaf surfaces.

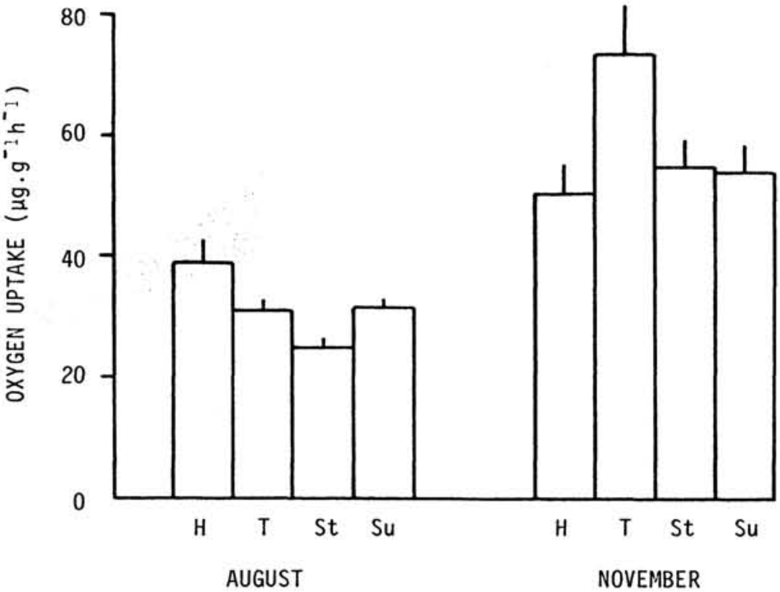
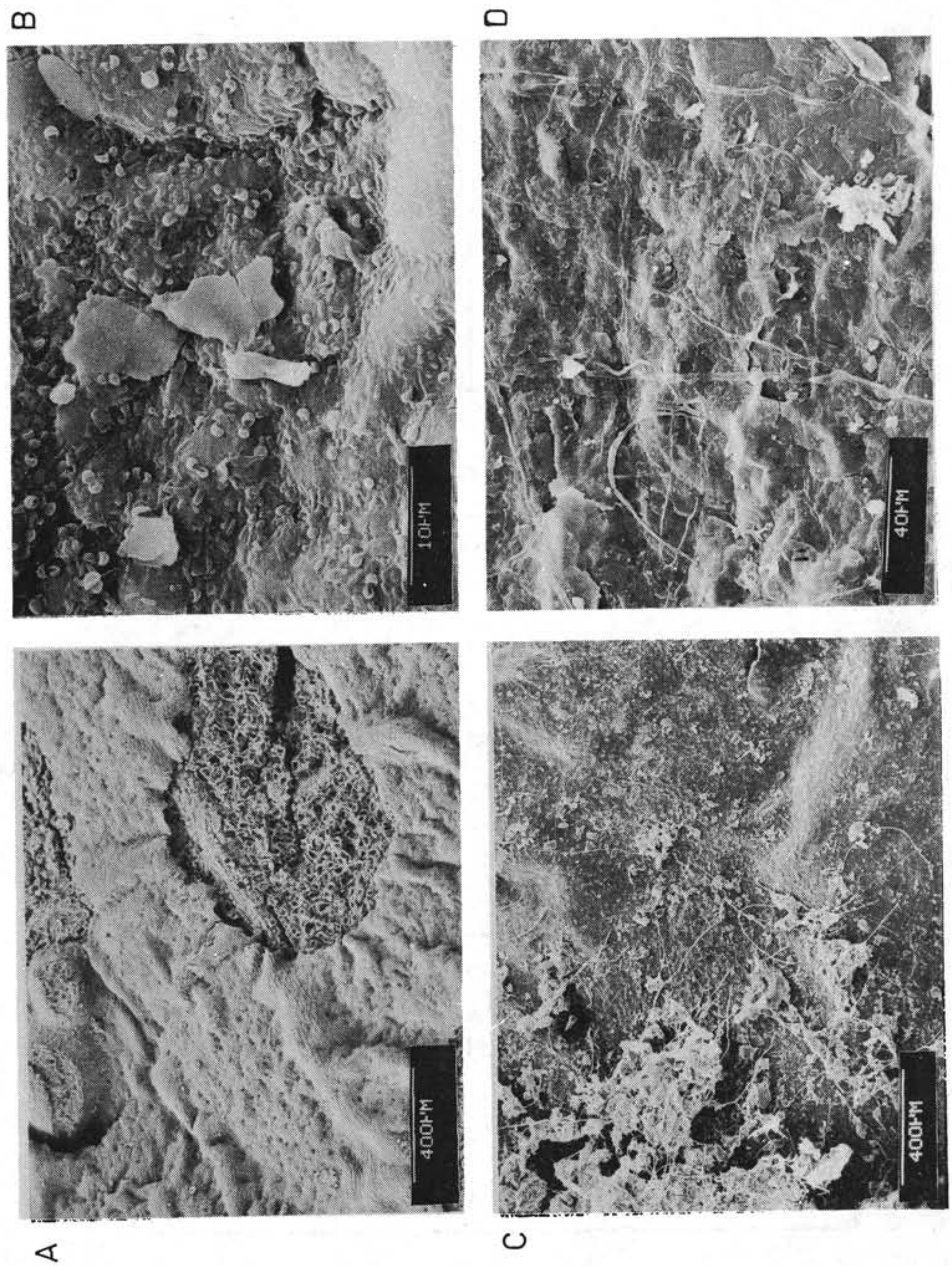


Fig. 2 Respiration rates ($\bar{x}$ + 1 SE, n = 5) of microbial communities associated with leaves removed from the four study streams in August and November 1985 (148 and 244 days incubation, respectively). H, Hidden Creek; T, Toilet Stream; St, Steep Creek; Su, Suspect Stream.

TABLE 1 Mean annual pH of stream water and decay coefficients (-k) and half-lives (t_{50}) of kamahi leaves incubated in 1 mm mesh bags in the four study streams. Decay coefficients and half lives were calculated from the least squares fit of data including (no parentheses) and excluding (parentheses) day 0.

	pH	-k	t_{50} (days)
Hidden Creek	7.5	0.0039 (0.0043)	176 (163)
Toilet Stream	7.3	0.0034 (0.0035)	203 (198)
Steep Creek	4.9	0.0026 (0.0022)	270 (321)
Suspect Stream	4.7	0.0022 (0.0014)	321 (480)


A
B
C
D
400µM
10µM
400µM
40µM

COLONISATION BY INVERTEBRATES:

Twenty-nine invertebrate taxa were taken from leaf bags at the four sites (Table 2). Most (19) occurred in bags at Toilet Stream and least (8) at Suspect Stream. Chironomids were common at all sites and in the brown-water streams they accounted for about 90% of the total bag fauna. In contrast, the hydrobiid snail, *Potamopyrgus antipodarum*, was by far the most common colonist at Toilet Stream whereas the stonefly *Austroperla cyrene* shared dominance with chironomids at Hidden Creek. Larvae of *A. cyrene* and *Olinga feredayi*, the commonest caddisfly at Hidden Creek, are known to eat decomposing leaves (Winterbourn, 1982), whereas *Triplectides* sp., the most abundant trichopteran at Toilet Stream, is an obligate shredder of leaves and wood.

Gut content analysis showed that *Oeconesus* sp., which was found in small numbers in bags at Toilet Stream, also can eat coarse particulate organic matter.

DISCUSSION

Although a number of workers have examined the effects of low pH on organic matter processing in streams, few investigations have been made in "naturally" acid waters. The studies of Otto & Svensson (1983) and Mackay & Kersey (1985) are two exceptions and both found that, as in many anthropogenically acidified streams, leaf litter breakdown was inhibited by low pH. Reduced microbial activity appears to be a major factor contributing to slower breakdown rates under acidic conditions (e.g., Mackay & Kersey, 1985; Allard & Moreau, 1986), and Chamier (1987) suggested that the disruption of microbial enzyme systems involved in leaf degradation may be the reason for this.

Breakdown rates of kamahi leaves in the four South Westland streams fall into the "slow" category ($-k < 0.0050$) of Petersen & Cummins (1974), along with species such as white oak (*Quercus alba*) and quaking aspen (*Populus tremuloides*). Indeed, $-k$ values for kamahi leaves enclosed in 1 mm mesh bags in the brown-water streams are amongst the slowest recorded for tree leaves (Webster & Benfield, 1986). Breakdown rates at the clear-water sites were similar to that ($-k = 0.0044$) obtained by Davis & Winterbourn (1977) for leaves of mountain beech (*Nothofagus solandri* var. *cliffortioides*) enclosed in 1 mm mesh bags in Middle Bush Stream, Cass (pH 6.7-7.1).

Most of the initial rapid loss in leaf weight (28 %) observed on day 42 could be attributed to rapid leaching of soluble compounds in the first few days of the experiment (Kaushik & Hynes, 1971; McCammon, 1980). Because leaf shredding invertebrates were absent from bags in Suspect Stream and constituted only a minor proportion (0.6%) of the fauna in bags taken from Steep Creek, post-leaching weight losses at these sites could be attributed primarily to microbial decomposition. However, large particle detritivores made up about 38 and 8% of the numbers of animals in bags from Hidden Creek and Toilet Stream, respectively, indicating that post-leaching weight losses at these sites were the result of microbial breakdown and invertebrate feeding.

Fig. 3 Scanning electron micrographs of leaf surfaces after 148 days in 1 mm mesh bags in Hidden Creek (A), Toilet Stream (B) and Steep Creek (C and D). Fungi were the dominant microbial colonists on leaves from the brown-water sites (e.g., Steep Creek) but these often were associated with amorphous material on the leaf surface (C). In contrast, leaves from the clear-water sites (Hidden Creek and Toilet Stream) were relatively clean and upper tissue layers had been removed in places (A). Bacteria appeared to be the most common microbes on leaves at these sites (B).

TABLE 2 Percentage composition of the invertebrate faunas colonising leaf bags removed from the four sites in August, November and January (all bags combined).

	Hidden	Toilet	Steep	Suspect
INSECTA				
EPHEMEROPTERA				
Deleatidium spp.	3.4	6.3	1.3	0
Mauiulus luma	0.4	0.3	0	0
Ameletopsis perscitus	0	0	0.2	0
PLECOPTERA				
Austroperla cyrene	30.3	1.3	0.6	0
Cristaperla fimbria	1.1	0	0	0
Spaniocerca longicauda	1.9	7.5	0	0
Stenoperla maclellani	3.4	0.9	0	0
Zelandobius confusus	0	0	0.8	0
TRICHOPTERA				
Olinga feredayi	8.0	0.6	0	0
Oeconesus sp.	0	0.6	0	0
Philorheithrus agilis	3.1	1.3	0	0
Triplectides sp.	0	5.7	0	0
Rakiura vernale	0	0	0.2	0
Zelolessica sp.	0	0	0.2	0
Hydrobiosis sp.	0.4	0	0	0
Psilochorema sp.	0	0	0	0.5
Hydrobiosidae indet.	0.8	0	0	0
Polyplectropus sp.	0	0	0.4	0
DIPTERA				
Chironomidae	33.0	15.1	92.1	88.8
Empididae	1.1	0.3	0	0.5
Eriopterini	0	0.3	0	0
Ceratopogonidae	0	2.2	2.4	3.7
Paralimnophila skusei	0	0.3	0	0
Muscidae	0	0	0.2	0
GASTROPODA				
Potamopyrgus antipodarum	0	50.6	0	0
CRUSTACEA				
AMPHIPODA	0	0.9	0	1.1
OSTRACODA	1.1	0.3	0.4	0.5
OLIGOCHAETA	10.7	5.0	0.9	4.3
ARACHNIDA				
ACARINA	1.1	0.3	0.4	0.5
Total numbers	261	318	533	188

Densities of fungal hyphae were greater on leaves from the acid, brown-water streams on the one date (day 148) that leaf surfaces were examined under the SEM. Hendry et al. (1976) and van Frankenhuyzen & Geen (1986) also noted increases in fungal biomass on organic matter from acidified waters, but Chamier (1987) found significantly more aquatic hyphomycetes and bacteria on leaves from slightly acid (pH 6.6-6.8) than strongly acid (pH < 5.5) streams in the English Lake District. Fungi are thought to be most important in the initial stages of leaf breakdown (Suberkropp & Klug, 1981). As the macerating activity of fungi and the feeding of invertebrates increase leaf surface area in the later stages of decomposition, bacteria are believed to have a competitive advantage over fungi and thus dominate microbial communities on more decomposed leaves.

In the present study, bacteria were more common on leaves from the clear-water streams on day 148 (Fig. 3). Subsequent work on kamahi leaves at different stages of decomposition has confirmed that fungi are abundant in the brown-water streams whereas microfloras at the clear-water sites are dominated by bacteria (authors' unpubl. data). Similarly, Davis & Winterbourn (1977) concluded that fungi played a minor role compared to bacteria in the microbial breakdown of beech leaves in Middle Bush Stream.

Respiration rates for leaf microflora measured in the present study (24.8-73.4 $\mu gO_2.g^{-1}.h^{-1}$) are lower than those obtained by Allard & Moreau (1986) (70-200 $\mu gO_2.g^{-1}.h^{-1}$) for alder (*Alnus rugosa*) and sweet gale (*Myrica gale*) leaves incubated at 12-19°C in experimental stream channels, and by Rounick & Winterbourn (1983b) for mountain beech leaves from Middle Bush Stream (112-294 $\mu gO_2.g^{-1}.h^{-1}$). Allard & Moreau (1986) found that O_2 consumption was significantly lower in acidified (pH 4.0) than unacidified (pH 6.2-7.0) channels (after about 70 days incubation) whereas in our study no distinct pattern between environments was evident after 148 and 244 days. However, oxygen uptake need not be a reliable indicator of decomposition rate since some microbes (e.g., some of the fungi visible in Fig. 3C) appear to use leaf surfaces primarily as a substratum and have little or no involvement in leaf breakdown.

A problem with the use of 1mm mesh bags in the present study was that it did not allow free access to and from enclosed leaves for all invertebrates. Small insect larvae were able to enter the bags freely, but some appeared to grow to such a size that they were unable to leave. The effect of this on leaf breakdown may have been counterbalanced to some extent by the exclusion of large larvae from the bags and may contribute to the between-bag variability in leaf weight losses shown in Fig. 1. Nevertheless, it is clear that large particle detririvores were largely responsible for the faster breakdown rates of kamahi leaves recorded at the clear-water sites.

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